EXPLANATION OF THE PLATES.

PLATE XX.

Figs. 1, 2. *Bairdia dubia.* × 84.
3, 4. *Cythere crispata.* × 110.
5, 6. „ *cingulata.* × 110.
7, 8. *Cythereis deformis.* × 84.
9, 10. *Argillœcia affinis.* × 84.

PLATE XXI.

Figs. 1, 2. *Loxoconcha decipiens.* × 90.
3, 4. „ *obesa.* × 84.
5, 6. „ *subalata.* × 115.
Fig. 7. *Cytherideis subulata*, var. *crenulata.* × 84.
Figs. 8, 9. *Paradoxostoma gracile.* × 84.
10–13. *Xestoleberis latissima.* × 110.

PLATE XXII.

Figs. 1–3. *Xestoleberis nigromaculata*, ♀ ♂. × 84.
4, 5. *Cytherura cribrosa.* × 100.
6. 7. „ *maculosa.* × 100.
8, 9. „ *fossulata.* × 100.
Fig. 10. *Sclerochilus lævis?* × 84.
Figs. 11, 12. *Cytherella ovalis.* × 100.

28. On Colour and Colour-pattern Inheritance in Pigeons. By J. LEWIS BONHOTE, M.A., F.L.S., F.Z.S., and F. W. SMALLEY, F.Z.S.

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(Plates XXIII.–XXVI.*)

The following is a preliminary account of some experiments undertaken by the authors to throw some light on the inheritance of colour and colour-pattern in Pigeons. These experiments are being continued, as the matter is a long and complicated one and will of necessity take several years to complete.

The experiments on certain colours and colour-patterns, however, have been practically completed, and the results are briefly given below.

Apart from the practical knowledge given in books on fancy pigeons, no serious work has been published on the inheritance of colour in Pigeons except Darwin's (Animals and Plants under Domestication, vol. i. p. 197 *et seq.*, 1868 ed.), and a recent paper by Mr. Staples-Browne (P. Z. S. 1908, p. 67).

The information in the 'fancy' books, valuable as a guidance for practical breeding, is of little utility from the scientific point of view, as details of pedigrees are often lacking. The work of Darwin we have also had to pass over, for the present, owing to the difficulty of making out with any accuracy the exact colour of his birds from the terms he used. It is by no means intended to imply inaccuracy in that most accurate of observers, but the 'fancy' terms for colours, though well understood by breeders, do

* For explanation of the Plates see p. 619.

not readily admit of a scientific interpretation unless the birds themselves can be seen; frequently the same colour (from a scientific point of view) may be known by different names according to the particular breed of pigeons that may be under discussion.

Darwin's experiments related chiefly to "reversion," *i.e.* the reappearance of the blue colour when distantly related breeds of pigeons were crossed, and although our work has not been on the same lines, the study of the blue colour should, none the less, bear out the results arrived at years ago. We are not unmindful of this, and for that very purpose hope to mate up several pairs to test Darwin's conclusions.

Lastly there is Mr. Staples-Browne's recent paper, in which he has attempted to repeat Darwin's experiments. This paper we have been through very carefully, and find that in the main it agrees with our results, but one or two little difficulties have to be met, such as the occurrence of a Dun in Exp. 27, the absence of Blacks in Exps. 9 & 11, the large proportions of white in Exps. 16–23 and 30, and the occurrence of white feathers on a homozygous blue.

We have no doubt that further work will clear up these slight difficulties, which do not, however, greatly affect the main result; in fact a possible explanation of some of them has already suggested itself to us, but the discussion of these is best deferred until the results of our matings on the same lines as Darwin and Staples-Browne have been obtained.

The majority of the birds used have been highly bred Dragoons, but in a very few cases a Homer cross has been introduced.

The characters dealt with in this paper are:—

(i) Colour-patterns, *i.e.* Chequering, Grizzle, and Mealy.
(ii) Colours, *i.e.* Blue and Silver, with White and Red in those cases where it is connected with Grizzle and Mealy.

Before detailing the experiments, however, it is necessary to have a clear understanding of the terms used.

(i) *Chequering.* This is a pattern chiefly confined to the wing-coverts, in which each chequered feather has a light coloured V-shaped patch at its distal end, the apex of the V being nearest the base of the feather (see Pl. XXVI. fig. 1). The general appearance of a good chequered bird is shown in Pl. XXIII. fig. 3, but it must be understood that scientifically and in the experiments we have carried out, a bird has been considered as chequered when it showed the characteristic markings on its wings.

(ii) *Grizzling.* A grizzled feather is one in which the barbs are partially white and partially coloured. This pattern is not restricted to any particular part of a bird, but grizzled feathers may be found in any feather tract including the remiges and rectrices.

On a grizzled bird (*i.e.* a bird with grizzled feathers) whole coloured feathers are generally found as well as feathers splashed with white (Pl. XXIV. figs. 1 & 2;

Pl. XXVI. figs. 2 & 4). The term 'Grizzle' is restricted in the 'fancy' to birds whose pigment is Blue grizzled with White.

(iii) *Mealy.* From the pattern point of view a Mealy is identical with a Grizzle but the White coloration is to a greater or lesser extent replaced by Red. A Mealy (for Mealy feathers see Pl. XXVI. figs. 5 & 6; the birds are figured on Pl. XXV.) may therefore show *Blue* and *Red*, or Blue, Red and White.

(iv) *Blue* (Pl. XXIII. fig. 1) is the colour of the Wild Rock Pigeon, although in domestic breeds the rump is not necessarily white. In a Blue Chequer (Pl. XXIII. fig. 3) the light apical portions of the feathers are of the typical blue colour, the rest of the feather and the general appearance of the bird being very much darker. A very dark Blue Chequer is almost black, but this black is usually dull and must not be confused with the glossy black (beetle-black) characteristic of a pure black pigeon.

(v) *Silver* is a *very* pale blue with black bars and "dun" flights. In a Blue pigeon the flights are black (Pl. XXIII. fig. 2).

(vi) *Red.* A Red pigeon is deep red all over including the flights and tail. In a Red Chequer the dark portion of the feathers are of the normal red and the light apical spots white. The flights and tail are white.

It must be remembered that all these varieties show considerable differences in shades of colour, and in the intensity and abundance of the pattern markings. In this paper, however, we do not propose to enter into these details, important as they are. Our object for the present is to separate those characters which follow apparently a Mendelian inheritance, from those whose mode of inheritance is different. This paper therefore will only deal with Mendelian inheritance, except to note in a few cases where that inheritance is apparently subservient to other causes. None the less these differences of shade and amount of pattern do obviously follow a definite law of inheritance, and they are by no means being disregarded by us, nor are we without hope of being able at some future time to attempt some explanation of the laws which govern their inheritance.

We may point out further that in the case of Mealies and Grizzles (*i.e.* where *normally* there should be a small amount of white), there is a great tendency to breed out in the course of a few generations to practically pure white with only a few coloured feathers. Our results, as far as they have gone, seem to show, however, that these nearly pure white birds are still transmitting to their offspring the colour which characterised their parents and grandparents.

Blues and Silvers.

Blue is dominant to Silver.

A careful analysis of our results shows that Silver is in reality a dilute Blue and that the colour factor in both is identical. The allelomorph is therefore concentration and dilution (c and d) of which the former is dominant.

Blue may therefore be represented as BBcc or BBcd, where B represents the blue colour factor. Silver must therefore be represented by BBdd.

Blues are said to almost always breed true, that is to say, that they never throw any Silvers—this idea owes its origin, however, to the fact that those Blues which are impure dominants (*i.e.* containing the factor d) are of a poorer colour than the pure Blues and have in consequence long been rejected by fanciers, so that a race of pure dominants has thus been evolved *. Several of our matings show that Blues or Grizzles that are heterozygous as regards c and d will throw Silvers†.

The following are the results of our matings for these particular characters, with the exception of Experiment 83, which is introduced to show the reappearance of Silver from two heterozygous Blues.

Exp.‡ No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.	Result.
83.	00/61	Grizzle	*BBcdGg*	—	02/126	Blue	BBcdgg	—	3 B 1 S.	6 B 2 S
148.	04/70	Silver	*BBdd*	—	04/21	Silver	BBdd	—	All S	— 5 S
149.	05/96	,,	*BBdd*	—	05/51	,,	BBdd	—	,,	— 3 S
150.	07/4	,,	*BBdd*	—	06/56	,,	BBdd	—	,,	— 5 S
151.	05/96	,,	*BBdd*	—	05/21	,,	BBdd	—	,,	— 1 S
152.	03/5	,,	BBddgg	83	04/140	Grizzle	BB*cc* or *cd*	157	All B or Equality	1 B 1 S
153.	04/10	,,	BBdd	140	{04/10 revd.}	,,	BB*cc* or *cd*	77	,, ,,	7 B —
154.	04/14	Grizzle	BB*cc* or *cd*	96	07/52	Silver	BBdd	151	,, ,,	4 B 2 S
155.	08/1336	Silver	BBdd	148	08/1368	Grizzle	BB*cc* or *cd*	137	,, ,,	6 B —
156.	03/5	,,	BBdd	83	01/50	Blue	*BBcc*	—	All Blue	3 B —
157.	03/6	,,	BBdd	83	02/31	,,	*BBcc*	—	,, ,,	4 B —
158.	05/95	Blue	BB*cc* or *cd*	105	05/51	Silver	*BBdd*	—	,, ,,	2 B —
159.	06/13	,,	BB*cd*	65	06/66	,,	BBdd	—	Equality	1 B 1 S
160.	03/5	Silver	BBdd	83	02/126	Blue	BBcd	—	,,	3 B —
161.	07/4	,,	BBdd	—	06/67	,,	BBcd	158	,,	3 B —
162.	04/52	Blue	BBcd	156	06/56	Silver	BBdd	—	,,	2 B 2 S
163.	08/1335	Silver	BBdd	148	08/1387	Blue	BBcd	154	,,	3 B 3 S

When the Gametic Formula is in italics it implies that it is not *definitely* known. Only the characters under immediate consideration are given in the Gametic Formula.

* See also remarks on chequering.

† We must, however, point out here that in Mr. Staples-Browne's experiments, one or two blues, apparently heterozygous, behaved as homozygous and *vice versa*.

‡ With regard to the numbering of Experiments—the numbers refer to our stud book, and rather than number the experiments quoted successively in this paper, it was thought best to have only one set of numbers so that references might at any future time be easily made without risk of confusion.

From these matings we see that:—

(i) Silver to Silver (Exps. 148 to 151) gives nothing but Silver, according to expectation.

(ii) Blue to Silver (Exps. 152 to 159) should give nothing but Blues or Blues and Silvers according to whether the Blues are heterozygous or not, and we see that when our knowledge of the gametic formulæ of the parents was known for certain, the results were in exact accord with expectations, and no results antagonistic to possible expectations occurred.

(iii) Heterozygous Blues to Silvers (Exps. 160–163) should give equality of Blues and Silvers. In the case of Exps. 160 and 161 no Silvers appeared, but the numbers bred were very small. In the other experiments. exact equality was reached, so that we may well assume that a continuation of the other experiments would have led to the appearance of some Silvers.

(iv) Heterozygous Blue × Heterozygous Blue should give Blues and Silvers in proportion of 3 : 1, which was the exact result of this mating (Exp. 83).

The results therefore show clearly that Silver is recessive to Blue. The arguments showing that the difference between these colours is one of concentration and dilution (rather than a difference of the colour factor itself), depend on the study of this dilution factor, which, as it concerns the inheritance of other colours and shades, not dealt with in this paper and at present only imperfectly understood, is best deferred for the present. Its discussion in no way affects the proof of the dominance of Blue over Silver.

Chequering.

Chequering is dominant to pure colour. It is difficult to realize therefore how it can have originated, since the *typical* wild pigeon shows no such markings. At the present time, however, in many parts of the country wild birds show chequering, but it seems more than likely that in these cases the marking has been introduced by a cross with the domestic bird, as most of the Wild Rocks in this country are now intermixed with feral ones. Once this cross had been effected the chequering would of course frequently show itself.

In direct contradiction to the foregoing remarks the following fact is worth noting. Some years ago a pair of pure wild birds was taken by one of the authors from a remote district in the West of Ireland. All the wild pigeons seen (and there were no tame ones within a radius of at least 30 miles) were purely typical Blue Rocks. This pair bred in an aviary for five or six seasons, producing only typical wild birds like themselves. Two seasons ago (in 1909) an attempt was made to establish some of their progeny as semi-wild birds and they were allowed to fly at liberty from a dove-cot. One pair remained and reared several young, one of which proved to be chequered!

Scientifically this result is of but little value, as the hen bird *may* have made a chance mating with a chequered pigeon; on the other hand, the youngster was in every other respect (shape and size) a typically wild bird. Unfortunately it met with an accident, so that we have not been able to breed from it.

Unsatisfactory as this case is, it is obvious that the chequering must in the first place have originated from the Wild Rock Pigeon, and the above is probably a good example of its arising as a mutation.

A further explanation may possibly be found in the fact that the chequering cannot show itself except in the presence of two shades of colour, and that it may be present in many of the pure wild birds but cannot show itself until the colour factor producing the two shades is present, when the chequering will immediately appear.

This, however, in no way affects the main issue, namely that when once a Chequer has been produced it is dominant to the pure colour. The mating of two Chequers should therefore produce Chequers or Chequers and Self-colour, according to whether the birds are homozygous or heterozgyous for that character.

As in the case of the Blues, so in the case of the Chequers it appears that fanciers, by continually selecting the best birds for breeding, have unconsciously been selecting only homozygous birds, with the result that only pure Chequer dominants are to be found in certain strains. We have for instance accurate records of 57 matings (Exps. 1–49; 169–172; 175–178) of Chequer to Chequer from which 229 young were produced, and all these without exception were Chequers like their parents. It therefore became essential to carry out further matings with birds that were known to be heterozygous in order to test the dominance of the Chequer character. This has been done in the matings detailed below, the results of which, as will be seen, approximate very closely to the Mendelian expectation.

Exp. No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.	Result.
174.	06/104	Red Chequer.	Xx	173	06/82	Blue.	xx	122	Equality	2 Ch : 2 B
196.	650	Blue Chequer.	Xx	14 S-B	06/69	Grizzle.	xx	153	„	3 : 2
197.	07/*b*	Grizzle Chequer.	Xx	196	08/*c*	Blue.	xx	196	„	5 : 3
198.	07/*a*	Grizzle Chequer.	Xx	196	08/*d*	Blue Chequer.	Xx	196	3 : 1	2 : 2
199.	07/*b*	Grizzle Chequer.	Xx	196	08/13	Grizzle.	xx	196	Equality	2 : 0
200.	08/19	Blue Chequer.	Xx	197	08/22	Blue Chequer.	Xx	197	3 : 1	10 : 1 *
201.	09/533	Blue Chequer.	Xx	197	08/36	Blue Chequer.	Xx	198	3 : 1	3 : 3*
203.	08/24	Grizzle Chequer.	Xx	198	08/30	Grizzle.	xx	197	Equality	7 : 2

Chequering and its absence are represented by X and x.

* Matings for the purpose of testing the extracted recessives from Exps. 200 and 201 have been undertaken this year (1911), and prove the recessives to breed true.

It should perhaps be noted that although the individual matings show, considering the small numbers, a very close approximation to the expected results, yet at the same time the tendency to vary from the anticipated results is all in one direction, viz. to a greater number of Chequered birds. This is most marked in those matings where equality was expected, for of the 28 birds bred, 19 were Chequers; in those cases where the expectation was 3 : 1, 21 birds were bred of which 15 were Chequers, which is approximately correct. It is possibly due as much to this tendency as to the unconscious selection by breeders, that this character has become perfectly true and stable in some strains. As pointed out in the earlier portion of this paper, we are restricting our remarks for the present to the consideration of the Mendelian inheritance of certain characters, and that theory seems to fit in well with the main lines of inheritance as borne out by the facts. None the less it is equally evident that there are other factors at work, which are able to modify to some extent the results anticipated by the Mendelian hypothesis. In addition to these definite matings we have also notes of 6 matings Chequer to pure colour (Exps. 164–168, 173) which gave 19 birds all chequered. In this latter set of matings most of the Chequered parents were birds used in or bred from the Chequer to Chequer matings; and therefore this adds further proof that all those birds were homozygous dominants, as otherwise we should have expected some self-coloured birds to appear as they did in Exps. 174–203 (p. 606).

It may be as well to mention here that although some of the matings referred to in this paper were not undertaken with the special purpose of bringing out the facts which they are used to interpret, yet they have all been conducted by one of the authors in person. Special matings have, however, been made in every case to prove the inheritance of the characters discussed *.

Grizzling.

Grizzling is dominant to Chequering and hence also to pure colour. It probably originated from the cross between Blue and White, although such matings usually give splashed birds, owing probably to the true Grizzle character, in which individual barbs show both white and blue, being absent. Cases, however, are known in which the cross between pure White and pure Blue have produced Grizzles, and in these cases there is little doubt that the Grizzle character must have been present in one or both of the parents but was unable to show itself owing to the bird containing only one colour. Once, however, the Grizzle has shown itself, the White and Grizzle characters seem to combine together and to have a common inheritance. Furthermore, as already stated, Grizzles when bred together tend usually, but not invariably, to show an increase of white in successive generations

* Mr. W. Bateson has stated (Mendel's Principles of Heredity, p. 43 (1909)) that chequering is dominant to its absence; on writing to him for a reference to the source of his statement, he says that he had in mind some experiments of Mr. Staples-Browne, which have, however, not been published.

till eventually some birds will be produced showing only one or two coloured feathers. This matter, however, we shall not discuss at present.

For our present purpose we may ignore the White character, assuming that it is always present and inherited in common with the Grizzle. The gametic formula, therefore, of a grizzled bird will be BBcc or cd GG or Gg, where B is the Blue colour, c & d concentration or dilution (the combination dd producing a bird known as a Silver Grizzle), and G & g the presence or absence of Grizzle. Therefore from the crossing of two Grizzles we may either get all Grizzles or Blues and Grizzles, according to whether the birds are homozygous or heterozygous to the Grizzle character. Under the term Blue we here for simplicity's sake include Silver.

Again, as in the case of the Chequers, the results from pedigrees are apt to be misleading owing to the difficulty of distinguishing the homozygous from the heterozygous birds; nevertheless such results entirely bear out our hypothesis, since, as regards the colours produced, the results are quite in accordance with expectations.

*Grizzle to Grizzle**.

Exp. No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.	Result.
74.	02/46 [*b*]	Grizzle	GG or Gg	—	99/104	Grizzle	GG	—	All G or 3 : 1	3 Grizzles
75.	03/21	,,	Gg	87	93/88	,,	GG or Gg	—	,, ,,	5 Grizzles
76.	00/21	,,	GG or Gg	—	63/7	,,	GG or Gg	—	,, ,,	4 Grizzles
77.	00/61	,,	Gg	—	99/104	,,	GG	—	,, ,,	7 Grizzles
78.	04/21	,,	GG or Gg	76	04/58	,,	Gg	94	,, ,,	4 G 2 B
79.	04/23	,,	Gg	99	06/102	,,	Gg	153	3 : 1	4 G 1 S
80.	04/1 rev.	,,	Gg	99	05/6	,,	Gg	109	3 : 1	1 G —
81.	04/12	,,	Gg	103	01/15	,,	GG or Gg	—	All G or 3 : 1	1 G 1 B
82.	06/88	,,	GG or Gg	78	04/58	,,	Gg	94	All G or 3 : 1	— 1 B

* As before, only the character dealt with is shown in the Gametic Formula.

Looking through these matings, we see that when both Grizzles and Blues should have appeared the expected proportion ought to have been 3 : 1, and the results give 10 : 5 or a rather large excess of Blues.

Grizzle to Blue.

These matings (Exps. 83–138, 152–155) may be divided into two groups: (1) those in which the gametic formulæ of both parents were known; (2) those in which, owing to the gametic formula of one parent being doubtful, two expectations were possible.

Certain of the Grizzles were known to be heterozygous: this was the case in 19 matings, in which therefore Grizzles and Blues should have appeared in approximately equal numbers. Altogether 64 young were reared, 37 Grizzles and 27 Blues, thus showing a slight excess of Grizzles.

Grizzle to Blue.

Exp. No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.	Result.
83.	00/61	Grizzle	GG or Gg	—	02/126	Blue	gg	—	All Gg or Equality	4 G 4 B
84.	04/27	Blue	gg	—	04/28	Grizzle	GG or Gg	—	,, ,,	5 G 1 B
85.	04/10	,,	gg	—	03/26	,,	GG or Gg	—	,, ,,	1 G —
86.	00/21	Grizzle	GG or Gg	—	02/35	Blue	gg	—	,, ,,	1 G 2 B
87.	00/6 rev.	Blue	gg	—	02/24	Grizzle	GG or Gg	—	,, ,,	2 G 4 B
88.	02/9	,,	gg	—	01/24	,,	GG or Gg	—	,, ,,	2 G 4 B
89.	02/37	Grizzle	GG or Gg	—	02/41	Blue	gg	—	,, ,,	1 G 2 B
90.	02/46 (*a*)	,,	GG or Gg	—	21	,,	gg	—	,, ,,	4 G —
91.	02/46 (*b*)	,,	GG or Gg	—	43	,,	gg	—	,, ,,	— 6 B
92.	03/31	Blue	gg	84	02/23	Grizzle	GG or Gg	—	,, ,,	— 5 B
93.	01/27	,,	gg	—	01/15	,,	,,	—	,, ,,	4 G 2 B
94.	03/19	,,	gg	86	01/24	,,	,,	—	,, ,,	2 G 2 B
95.	03/11	,,	gg	51	02/77	,,	,,	—	,, ,,	4 G 1 B
96.	01/13	,,	gg	—	01/28	,,	,,	—	,, ,,	4 G 1 B
97.	03/37	Grizzle	GG or Gg	—	02/38	Blue	gg	—	,, ,,	— 3 B
98.	03/20	,,	Gg	—	02/22	,,	gg	—	Equality	1 G 2 B
99.	01/11	Blue	gg	—	03/9	Grizzle	Gg	84	,,	5 G 1 B
100.	01/10	,,	gg	—	00/53	,,	GG or Gg	—	All Gg or Equality	— 1 B
101.	02/19	,,	gg	—	98/96	,,	,,	—	,, ,,	3 G 3 B
102.	02/34	Grizzle	GG or Gg	—	02/26	Blue	gg	—	,, ,,	— 1 B
103.	98/9	,,	,,	—	02/20	,,	gg	—	,, ,,	1 G 3 B
104.	00/6	Blue	gg	—	03/53	Grizzle	Gg	88	Equality	1 G —
105.	02/52	,,	gg	—	03/7	,,	GG or Gg	—	All Gg or Equality	2 G 4 B
106.	01/27	,,	gg	—	01/24	,,	GG or Gg	—	,, ,,	— 1 B
107.	02/46 (*b*)	Grizzle	GG or Gg	—	02/25	Blue	gg	—	,, ,,	1 G 5 B
108.	03/75	,,	,,	74	03/51	,,	gg	53	,, ,,	3 G 2 B
109.	02/46 (*a*)	,,	,,	—	03/23	,,	gg	53	,, ,,	2 G 5 B
110.	04/31	Blue	gg	59	03/9	Grizzle	Gg	84	Equality	2 G 1 B
111.	04/7	,,	gg	95	00/53	,,	GG or Gg	—	All Gg or Equality	1 G 3 B
112.	04/4	,,	gg	—	01/28	,,	GG or Gg	—	,, ,,	2 G 2 B
113.	03/29	,,	gg	88	02/77	,,	GG or Gg	—	,, ,,	3 G 3 B
114.	00/21	Grizzle	GG or Gg	—	04/84	Blue	gg	157	,, ,,	2 G 3 B
115.	04/3 rev.	Blue	gg	61	03/8	Grizzle	GG or Gg	—	,, ,,	1 G 1 B
116.	00/61	Grizzle	Gg	—	04/12	Blue	gg	61	,, ,,	6 G —
117.	05/14	Blue	gg	65	01/53	Grizzle	GG or Gg	—	,, ,,	3 G 5 B
118.	04/121	,,	gg	59	01/24	,,	,,	—	,, ,,	1 G —
119.	01/7	Grizzle	GG or Gg	—	02/22	Blue	gg	—	,, ,,	2 G 3 B
120.	02/46(*a*)	,,	,,	—	04/53	,,	gg	61	,, ,,	2 G —
121.	03/75	,,	,,	74	04/18	,,	gg	—	,, ,,	2 G 4 B
122.	02/46(*b*)	,,	,,	—	03/78	,,	gg	53	,, ,,	1 G 5 B
123.	04/4 rev.	Blue	gg	61	05/6	Grizzle	Gg	95	Equality	3 G 4 B
124.	04/93	,,	gg	61	01/53	,,	GG or Gg	—	All Gg or Equality	4 G 1 B
125.	04/115	Grizzle	Gg	104	04/120	Blue	gg	59	Equality	3 G 2 B
126.	04/133	,,	Gg	90	02/22	,,	gg	—	,,	2 G —
127.	04/52	Blue	gg	156	04/10 rev.	Grizzle	GG or Gg	77	All Gg or Equality	4 G —
128.	05/40	Grizzle	Gg	108	04/53	Blue	gg	61	Equality	3 G —
129.	05/119	Blue	gg	65	00/53	Grizzle	GG or Gg	—	All Gg or Equality	1 G 1 B
130.	02/46(*a*)	Grizzle	GG or Gg	—	04/27	Blue	gg	91	,, ,,	2 G —
131.	04/14	,,	Gg	96	06/87	,,	gg	123	Equality	4 G —
132.	05/92	Blue	gg	105	03/9	Grizzle	Gg	84	,,	1 G 1 B
133.	04/121	,,	gg	59	04/58	,,	Gg	94	,,	— 2 B
134.	05/96	,,	gg	105	06/22	,,	Gg	119	,,	1 G 2 B
135.	04/13	Grizzle	Gg	96	04/48	Blue	gg	—	,,	4 G 1 B
136.	06/57	,,	Gg	118	06/63	,,	gg	123	,,	— 1 B
137.	04/121	Blue	gg	59	04/58	Grizzle	Gg	94	,,	2 G —
138.	06/57	Grizzle	Gg	118	05/43	Blue	gg	113	,,	— 1 B
152.	03/5	Silver	gg	83	04/140	Grizzle	Gg	157	,,	1 G 1 B
153.	04/10	,,	gg	140	04/10 rev.	,,	GG or Gg	77	All Gg or Equality	7 G —
154.	04/14	Grizzle	Gg	96	04/52	Silver	gg	151	Equality	2 G 4 B
155.	08/1336	Silver	gg	148	08/1368	Grizzle	Gg	137	,,	2 G 4 B

In only 8 of the other matings did Blues fail to appear, and we may therefore consider that when they did appear the expectation should have been equality as before. Deducting therefore these 8 matings which only produced Grizzles, we have left 33 matings producing 156 young, 63 being Grizzles and 93 Blues. Since only one expectation is possible if both colours appear, we are justified in uniting the figures from these two sets of matings and treating them together. We find, therefore, that in the total we have 52 matings of Grizzle to Blue, which produced 220 young of which 100 were Grizzles and 120 Blues; and this proportion, although not exact, is not unreasonably far from the expectation (Equality), and certainly seems to show a Mendelian basis of inheritance.

If we digest the facts still further, we find that actual equality was reached in only 19 cases, and this by including the odd numbered broods where the deviation was not more than one.

We have, therefore,

Actual Equality reached in roughly			36 %	of the matings.
Blues outnumbered the Grizzles by more than one in			20 %	"
Grizzles	"	" Blues " "	14 %	"
Blues only, appeared in			18 %	"
Grizzles only,	"	"	14 %	" *

This, therefore, seems to show that while only a moderate percentage of matings gave the exact Mendelian expectation, the variation to one side or other of the mean is fairly evenly balanced, with however a slight but unmistakable tendency towards an overproduction of Blues; a tendency which was also shown in the Grizzle to Grizzle matings.

Thus, as in the case of the Chequers where we found the Mendelian proportions fairly well maintained, but with a distinct tendency to an overproduction of Chequers, so also in the Grizzles we see a similar tendency to an overproduction of Blues.

There remains for consideration the 8 matings in which only Grizzles appeared. Two of these may be at once dismissed as only one bird was reared, so that we have no hint as to the probable expectation. From the other 6 matings 25 birds were reared, so that there is a reasonable probability of a Blue having appeared were either of the parents heterozygous. Unfortunately for the simplicity of this reasoning, we find on investigating the matter more closely that although in 3 of these matings the same hen was used and we might therefore presume her to be homozygous, yet by her progeny in another mating (Exp. 109) she proved herself to be heterozygous. This then leaves only 3 cases out of 60 in which the Grizzle parent might be homozygous. So that again, just as we found in the Chequers and Blues an overwhelming proportion of homozygous birds, which we attributed to the unconscious selection of breeders, similarly in this case the

* This last calculation is of course exclusive of the 8 matings mentioned above, in which the gametic formula of the Grizzle parent was doubtful.

Exp. No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.	Result.
153.	04/10	Silver	gg	140	04/80 rev.	Grizzle	GG or Gg	77	All Grizzles or Equality	7 Gg . 0
196.	650	Blue Chequer	gg	148 B	06/69	Grizzle	Gg	153	Equality	3 Gg . 2 gg
197.	07/*b*	Grizzle Chequer	Gg	196	08/*c*	Blue	gg	196	,,	4 Gg . 4 gg
198.	07/*a*	,, ,,	Gg	196	08/*d*	Bl. Chequer	gg	196	,,	2 Gg . 3 gg
199.	07/*b*	,, ,,	Gg	196	08/3	Grizzle	Gg	196	Grizzles 3 : 1	2 GG or Gg . 0
200.	08/19	Blue Chequer	gg	197	08/22	Bl. Chequer	gg	197	No Grizzles	0 . 11 gg
201.	09/533	,, ,,	gg	197	09/36	,, ,,	gg	198	,, ,,	0 . 6 gg
202.	09/26	Grizzle	Gg	206	08/13	Grizzle	Gg	196	Grizzles 3 : 1	9 GG or Gg . 1 gg
203.	08/24	Silver Grizzle	Gg	198	08/30	,,	Gg	197	,, ,,	7 GG or Gg . 2 gg
204.	09/513	Almond Grizzle	GG or Gg	199	08/27	Al. Grizzle	GG or Gg	199	All G or 3 : 1	5 Grizzles
180.	02/46(*b*)	Grizzle	*Gg*	—	07/54	D. Mealy	Gg	179	3 : 1	11 GG or Gg . 1 gg
181.	08/1322	Silver Grizzle	Gg	154	08/1326	L. Mealy	GG or Gg	180	All G or 3 : 1	* 8 GG or Gg . 1 gg
182.	08/1376	,, ,,	Gg	154	08/1351	D. Mealy	GG or Gg	180	,, ,, 3 : 1	9 GG or Gg . 3 gg
183.	01/23	Grizzle	Gg	99	09/5468	D. Mealy	GG or Gg	182	,, ,, 3 : 1	3 GG or Gg . 3 gg
184.	04/14	,,	Gg	96	09/5466	D. Mealy	GG or Gg	181	,, ,, 3 : 1	1 GG or Gg . 2 gg
185.	09/1818	,,	GG or Gg	181	09/1815	Grizzle	GG or Gg	182	All G or 3 : 1 or Eq.	5 GG or Gg . 0
186.	09/5485	,,	GG or Gg	180	09/5487	,,	GG or Gg	181	,, or 3 : 1 or Eq.	2 GG or Gg . 1 gg
187.	09/1	,,	GG or Gg	180	09/1816	L. Mealy	GG or Gg	182	,, or 3 : 1 or Eq.	6 GG or Gg . 0
188.	09/1847	Light Mealy	GG or Gg	181	01/63	Blue	gg	62	All Gg or Equality	6 Gg . 0
189.	09/5467	Blue	gg	182	09/5465	L. Mealy	GG or Gg	181	,, ,, ,,	5 Gg . 0
190.	09/5486	Grizzle	GG or Gg	182	09/1863	L. Mealy	GG or Gg	180	All G or 3 : 1 or Eq.	4 GG or Gg . 0
191.	09/1843	Dark Mealy	,, ,,	180	09/4	D. Mealy	,, ,,	182	,, ,, ,,	6 GG or Gg . 0
192.	09/2	Blue	gg	181	09/1862	L. Mealy	,, ,,	180	All Gg or Equality	5 Gg . 0

* In this mating 2 almost pure white birds appeared; these have been considered as containing Grizzle owing to the presence of white, but as we are dealing with Mealies (see later) they may have been only gg.

number of the heterozygous birds largely predominates, and this is probably due to the fact that Grizzle × Blue is the commonest form of mating used by breeders to produce Grizzles.

We have no records of matings with 2 extracted (Grizzle-bred) Blues, but of Grizzle-bred Blues to Blue we have made 9 matings (Exps. 139–147). These matings produced 28 birds all Blue in accordance with the expectation.

In order to still further test our hypothesis we have carried out the foregoing experiments (see Table, p. 611).

The result of a scrutiny of these matings is sufficient to prove the Mendelian inheritance of the Grizzle character. In some of this last batch the expectation was well defined; in others—owing to the impossibility of distinguishing homozygous and heterozygous birds—the expectation was open to one or two, or in some cases three, interpretations. In those cases where the expectation was all Grizzles or Grizzles and absence, in proportion of 3 : 1, and only Grizzles were produced, we have concluded that one of the parents, at least, was homozygous—similarly, if any of the progeny in those cases lacked the Grizzle, we have presumed that the expected result should have been 3 : 1. On this basis we have tested the results and we find:—

Expectation.	No. of Matings.	Result.
All Grizzles	7	39 Grizzles.
3 : 1	7	32 Grizzles, 11 absence of Grizzle.
Equality	3	9 Grizzles, 9 absence of Grizzle.
No Grizzles	2	18 absence of Grizzle.
Equality or 3 : 1.........	2	5 Grizzles, 1 absence of Grizzle.

This last set of matings places therefore beyond doubt the Mendelian inheritance of the Grizzle character.

In the summary given above we have, however, left out Exp. 180, in which with an expectation of 3 : 1 or all Grizzles, 14 Grizzles and one pure Blue were produced. At the present moment, we can offer no reason for this considerable deviation from the expected result.

Grizzles and Chequers.

The Grizzle character is dominant to the Chequer, although, in almost every case, the heterozygotes may be easily recognised.

To test this inheritance we have made the following matings (see Table, p. 613).

These matings show fairly clearly the mode of inheritance, but from the smallness of the numbers the proportions of the different colours are not always in exact accordance with the expectation. It may be further noted that although, from the above reason, certain expected colours have as yet not occurred, on the other hand no unexpected colours or combinations have appeared. Thus we see that in Experiments 200 & 201 the recessive Chequers gave us, as expected, 14 Chequers to 4 Selfs, and *no* Grizzles; in Experiments 202 & 205 the pure Grizzles gave us, 11 Grizzles to 1 Self, and *no* Chequers. These two latter

Grizzles and Chequers.

Exp. No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.				Result.			
									CG	C	G	S	CG	C	G	S
179.	06/72	Red Chequer	Xxgg	173	04/11	D. Mealy	xxGg	......	1	1	1	1	–	3	1	1
193.	08/1558	„ „	Xxgg	——	08/1313	„	xxGg	135	1	1	1	1	–	2	1	2
194.	05/4	„ „	*XXgg*	——	09/5470	„	xxGg	193	1	1	0	0	2	2	–	–
195.	08/1525	„ „	*Xxgg*	——	09/5888	„	xxGg	155	1	1	1	1	2	2	–	4
196.	650	Blue Chequer	Xxgg	14 S–B	06/69	Grizzle	xxGg	153	1	1	1	1	2	1	1	1
197.	07/*b*	Grizzle Chequer	XxGg	196	08/*c*	Blue	xxgg	196	1	1	1	1	1	4	2	–
198.	07/*a*	„ „	XxGg	196	08/*d*	Blue Chequer	Xxgg	196	2	2	1	1	2	2	–	1
199.	07/*b*	„ „	XxGg	196	08/13	Grizzle	xxGg	196	2	1	2	1	2	–	–	–
200.	08/19	Blue Chequer	Xxgg	197	08/22	Blue Chequer	Xxgg	197	–	3	–	1	–	10	–	1
201.	00/533	„ „	Xxgg	197	08/36	„ „	Xxgg	198	–	3	–	1	–	3	–	3
202.	08/26	Grizzle	xxGg	206	08/13	Grizzle	xxGg	196	–	–	3	1	–	–	9	1
203.	08/24	Silver Grizzle	XxGg	198	08/30	„	XxGg	197	9	3	3	1	–	2	7	–
204.	08/27	Chequer Grizzle	XxGg	199	09/543	Chequer Grizzle	XxGg	199	9	3	3	1	–	–	5	–
205.	08/23	Grizzle.	xxGg	197	08/20	Grizzle	xxGg	197	–	–	3	1	–	–	2	–
206.	08/14	Blue Chequer	Xxgg	14 S–B	08/30	„	XxGg	197	2	2	1	1	–	1	1	–

X, x=Chequering and its absence; G, g=Grizzling and its absence. CG, C, G, S=Chequer Grizzle, Chequer, Grizzle, and Self.

(Exps. 194 & 195 were specially undertaken to produce a certain blend of CG (called Almond Grizzle) and for that purpose ♀'s showing "kiteyness" were chosen; in Exp. 193 the ♀ showed no "kiteyness" and no Al. G. appeared.)

matings (Exps. 202 & 205) may be compared with Exps. 203 & 204 *, matings of heterozygote Grizzles, where two Chequered birds turned up, although the whole number bred (12 birds) was far too small to give any hope of an approximation to the expectation being attained. Many of the Grizzles in these matings are very white, a factor which would tend to conceal the Chequer markings if present. It is more than likely therefore, that owing to this, some of these so-called Grizzles are in reality Grizzle-Chequers. Taking the Grizzles and Grizzle-Chequers (of Exps. 203 & 204) together, the expectation is 12 Grizzles and Grizzle-Chequers, 4 Chequers and 2 Self, and our result, 12 Grizzles and Grizzle-Chequers and 2 Chequers, is reasonably near the anticipation. The expectation in Experiments 179, 193, 195, 196 & 197, was an equality of Grizzle-Chequers, Chequers, Grizzles and Selfs, and the result 5 Grizzle-Chequers, 12 Chequers, 5 Grizzles, 8 Selfs, the only real discrepancy here being the overproduction of Chequers. This apparently merely confirms the conclusion come to in an earlier part of this paper, p. 607, which showed that there is apparently some factor which overrides the Mendelian inheritance, and leads to an increase in the number of Chequers produced.

Mealies.

A 'Mealy' may best be described as a Red Grizzled Pigeon showing Blue. The general appearance may be seen by reference to Plate XXV, and it should be noticed that it has the red bars and white flights characteristic of some varieties of red pigeons. When dealing with the Grizzle-character (G) we had to consider its relation to White, and we came to the conclusion that the White was not a colour factor complementary to Blue, but a separate allelomorph; so that the real gametic formula of a grizzled bird was made up of a compound allelomorph containing three characters—blue, white, and grizzling (B, W, G). For practical purposes, however, the W & G combine in their inheritance, and thus in the cases we have been considering they have, for convenience, been regarded as a single character (G).

In considering the inheritance of the Mealies, however, we must again pause to consider whether the factor for Red is to be treated as a colour factor, complementary therefore to Blue, or as complementary to the factor for White, or yet again as a separate allelomorph.

At first sight it would seem natural to consider it an alternative colour to Blue, but if this be the case a certain number of Self Reds should have appeared in our matings. None, however, were produced, though a certain number of Blues have been reared.

The same argument, though in a lesser degree, should hold good if it had an inheritance of its own, and we are thus driven to the conclusion that the Red is a complementary factor to the White. We have also had certain aberrant results (not dealt with in this paper) which point to a curious connection between these colours.

* This pair has produced both CG and pure Chequers this year (1911).

Finally, the study of the Mealy itself bears out this contention. A dark 'Mealy' differs from a dark 'Grizzle' in the fact that the white portions of the latter are replaced by red and the flights and tail instead of being black are white. In the Grizzles we noted that there was a great tendency for the white to increase till an almost pure white pigeon, showing only a few coloured feathers, was produced. Matings of Mealy to Mealy show an increase of the white, as is the case with Grizzles, till we eventually get a white bird showing a few coloured (Blue or Red) feathers. We must then come to the conclusion that in Mealies it is the white that is replaced by red, and *not* the blue. and therefore that a Mealy is a Grizzled bird in which the white is wholly or partially replaced by red.

We have had to go into this matter thoroughly as it offers certain difficulties, which cannot be entirely cleared up till the relationship of white and red have been further investigated; nevertheless the results of our experiments will offer no difficulty if the red is considered as an alternative factor to the white.

In our experiments with Mealies, one character has been present in all the matings, namely Blue, or in its dilute form Silver; we may therefore dismiss it from our calculations.

The only Chequer which appears (the one in fact by which the red colour was originally introduced) is shown in Exp. 179; the only Grizzle bird from that mating (Mealy ♂ 54), whose descendants form the large bulk of the Mealies, emphasizes the truth of his inheritance, since no chequered bird has appeared in spite of the large number bred.

The Grizzle character in the Mealy or Mealy bred birds we have already dealt with (Exps. 180–189, p. 611). The question therefore left us to consider in dealing with the Mealy inheritance is the question of Red and White. Red is apparently dominant to White, and in consequence a Mealy is dominant to a Grizzle.

The following matings (see Table, p. 616) show the inheritance of this character. It must be borne in mind that W & w are in this case practically equivalent to G & g in the earlier part of this paper. According to our present knowledge, when the Grizzle character meets with either white or red they combine in their inheritance to give either a Grizzle or a Mealy.

Taken as a whole, it will be seen that the results come remarkably near the expectation. In 5 of the 11 matings, in spite of the small numbers, the results *exactly* bear out expectations; and in all the others, with the exception of Exp. 181, the results are sufficiently near to leave little doubt that a continuance of the mating would have made them correct.

Taking the expectations and results together but omitting Exp. 181 we get:—

Expectation 2 M. 1 G. 1 S.	No. of Matings 4.	Result	18. 10. 9
,, 2 M. 2 G. 0 S.	,, ,, 5.	,,	11. 8. 0

in both of which sets there is a slight tendency to fewer

Exp. No.	♀	Ext. App.	Gametic Formula.	From Exp.	♂	Ext. App.	Gametic Formula.	From Exp.	Expectation.			Result.		
									Mealy	Grizzle	Self	Mealy	Grizzle	Self
180.	02/46 *b*	Grizzle	Ww	—	07/54	D. Mealy	Rw	179	2	1	1	9	5	1
181.	08/1322	Silver Grizzle	Ww	154	08/1326	L. Mealy	RW	180	2	2	0	7	2	1
182.	08/1376	„ „	Ww	154	08/1354	D. Mealy.	Rw	180	2	1	1	7	3	3
183.	04/23	Grizzle	Ww	99	09/5468	„	Rw	182	2	1	1	2	1	3
184.	04/14	„	Ww	96	09/5466	„	Rw	181	2	1	1	–	1	2
187.	09/1	„	Wr	180	09/4846	L. Mealy	RW	182	2	2	0	2	2	0
188.	09/4847	L. Mealy	WR	181	09/63	Blue	ww	62	2	2	0	3	3	0
189.	09/5467	Blue	wr	182	09/5465	L. Mealy	RW	181	2	2	0	2	1	0
190.	09/5486	Grizzle	rw	182	09/4863	„	RW	180	2	2	0	3	0	0
191.	09/4843	D. Mealy	Rw	180	09/4	D. Mealy	Rw	182	2	0	2	6	0	0
192.	09/2	Blue	rw	181	08/4862	L. Mealy	RW	180	2	2	0	1	2	0

W=White=Grizzle; R=Red=Mealy; w & r their absence.
Dark Mealy=presence of R and absence of W.
Light Mealy=presence of both R & W.
Blue= Self-colour, *i. e.* absence of both R & W.

Grizzles than one would expect. So that here again, although the numbers are small, the Mendelian proportion seems to be upset by a slight tendency in a definite direction.

The occurrence of a pure Blue (no. 2) in Exp. 181 is the *only* instance throughout the whole of our matings in which a colour, other than one which was expected, has appeared. Possibly the male parent of this mating (1326), although unlike his brother (1354) in external appearance, had in reality the same gametic formula. Such an occurrence would not be without precedent, as Mr. Staples-Browne instanced a homozygous Blue which showed a certain amount of white, and this ought to have indicated a heterozygous bird. The difference between these two birds (*i. e.* presence of white) is of the same nature, and in support of this suggestion the result of the mating—7. 2. 1—seems to be following on the same lines as Exp. 182.

There is one other possible suggestion for this abnormal result, and this is that the White or Red character may not have been inherited with the Grizzle.

The full formula of the parents on this basis is :—

♀ BBcd Gg [Ww]—♂ BBcd Gg [RW].

Now if the Grizzle has been independently inherited, we might get BBcdgg [RW, WW, wR, Ww] as the formula of one of the offspring, and the last character [RW etc.] might not in the absence of G be able to show itself, and this would give us what we got, namely a pure Blue. The result of the mating of this self-coloured bird (Exp. 192) throws no light on this, for if, as is quite possible, her mate was a homozygous Grizzle, no selfs would appear.

It must be understood that these are merely possible explanations, of which we are inclined to favour the first, but at present we have no definite proof in support of either.

For the rest, we claim that our hypothesis is so closely borne out by the facts that it may be accepted till further work confirms or disproves it : and until we are clearly able to differentiate between those characters which follow the Law of Mendel and those which are apparently governed by other laws.

In this paper we are only touching on the fringe of colour inheritance in Pigeons, as there still remains the question of Black, Dun, Red, Yellow, and White inheritance, on which we are at present continuing our researches. Our work, however, emphasizes the fact that there are three important problems which the Mendelian hypothesis fails to meet :—

(i) The differences of shades in the same colour;
(ii) The predominance of one sex in certain colours* ;
(iii) The gradual increase of the white in Grizzles and Mealies in successive generations;

* This most interesting question has not been dealt with in the present paper, as we have not yet fully investigated the results; but we may mention that a large proportion of the White Grizzles are ♀'s, and in the Light Mealies by far the larger number are ♂'s; we have also bred a certain number of Cream Mealies, and these have all been ♀'s.

and in addition to these the *apparently* large predominance of homozygous Chequers and heterozygous Grizzles.

These questions have been very much before us during the whole of our experiments, as indeed must be the case, for they cannot fail to bring themselves to the notice of every practical breeder.

At the present moment we do not consider it advisable to bring forward any attempted answers to these questions. Much more work yet remains to be done among the other colours, and until we know more of their inheritance any attempt to solve these problems would be premature. On the other hand, we are not without hope that the further experiments in which we are at present engaged may help to throw some light on these perplexing problems.

Summary.

This paper may strike a reader as having for its main object the confirmation of the Mendelian Laws; that, however, is by no means the case. Realizing that many details of inheritance did not entirely accord with the Mendelian theory, our object has been to extract, so to speak, from the results obtained by mating on Mendelian lines, that portion of them which clearly shows the Mendelian inheritance. The residue must, we submit, have been brought about by some law or series of laws, which overrides and modifies (externally at all events) the expected Mendelian results. By means of this extraction we are able to see the effect of that law or laws untrammeled by the effects of inheritance as ruled by the Law of Mendel, and thus we have been brought slightly nearer to an understanding of them.

Now this paper deals with the Mendelian inheritance of the characters considered; consequently all details of shades of colour, predominance of one sex in certain colours, and several other similar matters have been entirely omitted.

On the other hand, certain points such as the superabundance of Chequers in our Chequer matings and of Blues in the Grizzle and Blue matings, have had to be brought forward and the results are, we hope, sufficiently conclusive to prove to our readers that although the characters dealt with follow in the main on the lines of the Mendelian inheritance, yet it is equally certain that there is another factor which is able to dominate and influence that inheritance.

So far as the matter has been dealt with in this paper there is no evidence to show that the gametic inheritance has been affected. Except in one doubtful case (Exp. 181) we have not in the course of all our matings bred a single bird that was not a possible result of the mating under the strictest expectation of the Mendelian theory. What, however, we have been able to show is, that in certain cases a consistent deviation from the expected proportions occurs. It would thus seem at first sight as if some factor exists which has the power to influence but not to alter the gametic inheritance.

The Mendelian conclusions reached in this paper may be briefly summed up as follows:—

(1) Silver is dilute Blue.
(2) Blue is dominant to Silver.
(3) Chequering is dominant to its absence (*i. e.* a Self-colour).
(4) Grizzling is dominant to its absence (*i. e.* a Self-colour).
(5) Grizzling is dominant to Chequering; the impure dominants may however sometimes be easily distinguished.
(6) A Mealy is a Grizzled bird with the White wholly or partially replaced by Red.
(7) Red in a Mealy is apparently dominant to White, and hence a Mealy is dominant to a Grizzle.
(8) White and Grizzling when they have met combine together and have a common inheritance.
(9) Red combines with Grizzling in the same way as does White.

EXPLANATION OF THE PLATES.

Plate XXIII.

Fig. 1. Blue Pigeon.
2. Silver Pigeon.
3. Chequered Pigeon.

Plate XXIV.

Fig. 1. Dark Grizzled Pigeon.
2. White Grizzled Pigeon.
3. Grizzle and Chequer (Almond Grizzle) Pigeon—in nest feathering, showing adult feathers appearing on the wing-coverts. (Note chequering on the adult wing-coverts.)

Plate XXV.

Fig. 1. Dark Mealy Pigeon.
2. Light Mealy Pigeon.
3. White Mealy Pigeon. (Tricolor.)

Plate XXVI.

Feathers showing details of pattern-markings.

Fig. 1. Chequered feather.
2. Dark Grizzled feather.
3. Grizzle-Chequer feather, adult plumage, as shown in dark wing-coverts, Pl. XXIV. fig. 3.
4. White Grizzled feather.
5. Light Mealy feather. (Note white, red, and blue in some barbs.)
6. Dark Mealy feather. (Note absence of white.)

EXHIBITIONS AND NOTICES.

April 4, 1911.

Dr. Henry Woodward, F.R.S., Vice-President, in the Chair.

Sir E. Ray Lankester, K.C.B., F.R.S., F.Z.S., exhibited a special Supplement of the 'Field' newspaper dealing with the British non-migratory Trout, and called attention to this new medium for the publication of scientific observations requiring illustrations.

Dr. R. T. Leiper, F.Z.S., gave a demonstration of Nematode parasites obtained from animals in the Zoological Gardens during the year ending November 1910.

The collection contained a number of new forms, of which a systematic account will be published later. Among the more interesting of the known forms were *Rictularia plagiostoma* from a Palm-Civet, a number of species of *Polydelphis* from various Pythons, *Dicheilonema horrida* from the South American Ostrich, and *Dictyocaulus filaria* from the lungs of Sheep.

It was noticed that whereas intestinal parasites were almost wholly collected from animals that had not lived in the Gardens for more than six months, those of which the normal habitat and food were the internal tissues of the host occurred in animals that had been confined in the Gardens for several years. Thus, an undescribed *Filaria* was found in a Lemur after four years', and *Filaria australis* in a Wallaby after two and a half years' captivity.

In all these cases the number of parasites obtained was small, and could have had little or no effect upon the health of the host. There was a remarkable preponderance of female forms.

From these observations it appeared that the change of food and general conditions obtaining in the Gardens were unfavourable to the continued existence of the intestinal parasites an animal may harbour on its admission. The number of cases of auto- and re-infection during captivity was strikingly small, and bore testimony to the cleanly surroundings in which the animals were kept. In four cases only was there evidence of the occurrence of accumulative infection in the Gardens :—

1. A number of Giant Toads died from lung infection with *Rhabdias bufonis.*
2. The Wolves appeared to be heavily infected with *Ascaris canis.*
3. A Sheep died from pneumonic condition resulting from an intense infection with *Dictyocaulus filaria.*
4. The Tortoises had Oxyuriasis.

In all these cases repeated infection undoubtedly had followed from contamination of food and drink with fæces containing eggs of the parasite. The infection could be eliminated by steam sterilisation of the cages, or still more easily by changing the species of animal living in the particular paddocks or cages, for Helminthes were often peculiarly selective as regards their hosts, and those flourishing in one animal sometimes found it impossible to continue their life even in closely allied forms.

Mr. R. I. Pocock, F.R.S., F.L.S., F.Z.S., Superintendent of the Gardens, exhibited the newly born young of the Masked Palm-Civet (*Paradoxurus larvatus*), which had been born in the Gardens from a pair from Szechuen, presented to the Society by Mr. Thurlow Lay, and remarked that, although the specimen had died soon after birth, two other individuals composing the litter were alive and likely to do well. This was the first occasion on which the species had bred in the Gardens. The coloration of the

Text-fig. 147.

Inner aspect of abnormal left fore-leg of a newly born Masked Palm-Civet *Paradoxurus larvatus*.

p, pad; *s*, strip of naked skin; *c*, claw.

young resembled in a general way that of the adult, but was of a more generalised type, the black and white pattern of the head being less emphasized and the general colour of the body greyer with less yellow; the greater part of the tail and the lower portion of the limbs were sooty grey, the throat, chest, axillæ, belly, and the inside of the thighs being white. Of special interest was the presence of a pair of ill-defined dark stripes on the back and of very indistinct traces of pattern on the sides of the body. The head, which had the eyes and ears closed, was shaped very much like that of a wolf-pup. The tail was short-haired and tapering and as long as the body from the fore part of the shoulders backwards.

Special attention was drawn to a peculiar abnormality of the left fore-leg (text-fig. 147). The humerus appeared to be of normal length, but the lower arm was quite short, and there was no distinct elbow-joint; the paw, although freely articulated at the wrist, was axially rotated outwards so that its plantar surface looked inwards. It was furnished with a single large pad representing the large pad of the normal foot, and was armed with a terminal claw, a thin strip of naked skin passing from the claw to the pad.

[*Note added July 17th*, 1911.—The two specimens of the litter that survived grew with great rapidity as compared with dogs and cats, and almost equalled the size of their parents when three months old. Their eyes, however, opened, as in the former animals, about the ninth day from birth.]

Land Tortoises in the Seychelles.

The Secretary read the following dispatch from the Governor of the Seychelles, a copy of which had been kindly sent him by the Secretary of State for the Colonies, for communication to the Society.

Government House,
Seychelles,
1st June, 1910.

My Lord,

In view of enquiries made from time to time regarding the conservation of the breed of land tortoises of the islands in the Indian Ocean, I have the honour to append some notes condensed from the entries in the stud-book of the herd at Government House, Mahé. This book was opened by me soon after my arrival here in 1904, and contains records of the annual measurements of the specimens under my observation and of their habits.

2. In June 1904 I found a herd of 42 adult land tortoises, and 17 young ones hatched out in 1902 and 1903; these were duly marked, numbered and measured, and the particulars entered up in a new stud-book. The bulk of the herd had been purchased for the Government in 1892 from the late Mr. Nageon de l'Estang of Val des Prés, a proprietor of ancient family in the district of Anse Aux Pins, Mahé. The animals were then transferred to Curieuse Island, the property of the Crown, and were brought back to Government House in 1902.

3. In addition to this herd, there are two large males: No. 1. "Gordon," presented by the late General Gordon (of Khartoum) when he was stationed in Seychelles in 1881 after his transfer from the Cape; this is the largest land tortoise in Seychelles, and measures over the surface of the carapace 4′ $9\frac{1}{2}$″ and 4′ 8″. The

plastron measures 3′ 9″ × 2′ 9″. This is undoubtedly *Testudo elephantina* according to Dr. Günther's monograph. The next largest, No. 2. "Spurs," was presented by Mr. Spurs, now of Europa Island, a French possession in the Mozambique Channel: I am indebted for many of my most curious notes on the habits of all varieties of sea turtles and land tortoises to this gentleman, who is an educated man trained in habits of observation and has spent all his life among the islands of the Indian Ocean. The present dimensions of "Spurs" are 4′ 5″ × 4′ 4″ on the carapace and 3′ 7″ × 2′ 5″ on the plastron: he has grown slowly in breadth since 1904 but not in length. This remarkably fine specimen (the finest which Mr. Spurs has seen) is not of the *elephantina* variety, and resembles the *Testudo daudinii* of Dr. Günther's monograph.

These are probably the finest specimens living of their race. My recollection is that the *Testudo elephantina* which died at Colombo in 1900, of a recorded age of 155 years, was of larger dimensions. The large specimen at St. Helena was measured by Admiral Sir J. Durnford in 1907 as 4′ 6″ "fore and aft," but it is not certain whether this measurement included only the shell of the back.

4. The adult females, which are readily distinguishable in shape, are smaller than the males. The largest specimen in the collection (No. 5) reached its present dimensions—3′ 8″ × 3′ 10″ along the carapace and 2′ 8″ × 2′ 1″ along the plastron—in 1906, and has not grown during the last three years. Several others have rather smaller dimensions and have not grown since 1904.

The breeding season extends from January to April: the females carry their eggs for about 10 weeks and lay them in holes dug out by their hind legs and then covered over. The eggs in each nest vary in number from 9 to 25 and are white, round, and of the size of a lawn tennis ball. There may be two nests made annually by one female. Sea turtles lay a much greater number of eggs, *e. g.*, the green turtle 250 eggs at a time, and the hawks-bill turtle 100 to 150.

5. The young hatch out in about 120 to 130 days and work their own way out of the ground. At the Government House "parc aux tortues" about half of the eggs are unfertile; but in some years of drought, very few young ones appear, being unable (probably) to work their way up. They grow fast if well fed, and at four years old measure 1′ 6″ to 1′ 10″ in length and breadth of carapace. It is said that they attain full growth in 25 years. It is a local custom to mark off a young one at any birth in the family and to eat it at the child's wedding day. The meat is palatable and the liver is held to be a delicacy.

6. The number of young ones secured from 1904 to 1909 was 168; they are liable to be destroyed by rats before their shells harden. In a wild state at Aldabra practically all the young are destroyed by florentins (cranes), rats, and wild cats.

7. Through the courtesy of Admiral Sir John Durnford and Captain Dumas, R.N., six specimens from this herd have been presented to various institutions, *e. g.*, Groot Schuur, Pretoria. and the Zoological Society of London.

8. Owing to the difficulty in providing food for the increasing herd in the enclosures at Government House, I have drafted off—in March and May 1910—4 adult males and 18 adult females and 27 young ones of the "récoltes" in 1903, 1904 and 1905 to Long Island, a Crown property used as a quarantine station, where they are placed under the charge of the Guardians and where there is an ample supply of food.

9. "Gordon" shows likes and dislikes and is rather combative, having successfully bitten some visitors who presumed on his apparent lethargy, but generally the land tortoise shows little intelligence.

10. There have been no deaths among the adults during six years in the enclosures at Government House, but one male has been killed by a fall at Long Island, where they have shown themselves to be capable of swimming. The remains of tortoises found in the pits in the coral formation of islands in the Aldabra Group points to the falling into pits as one of the principal causes of death. They live apparently to an extreme old age—probably for 200 years. No plan will effectively prevent the final extinction of these curious survivals in a wild state in their natural habitats. The archives of Seychelles, Vol. i., published in 1909, are full of references to their size and number in Mahé and Praslin, where they were speedily destroyed by the early settlers. But their future existence is guaranteed by the fact that they breed in captivity and that several large herds besides that at Government House are kept and well cared for. It is a guarantee for their being taken care of that there is a sale for living specimens for zoological collections.

11. The best book in English on the subject is a monograph entitled "Gigantic Land Tortoises" by Dr. Günther, published for the British Museum about 1878. The names of the best known varieties of the larger tortoises and turtles are as follows:—

Of Aldabra: *Testudo elephantina.*

Of Galapagos: *Testudo nigra.*

Of Greece: *Testudo græca.*

Box Tortoise of Madagascar: *Pyxis arachnoides.*

Box Tortoise of North America: *Cistudo carolina* (Brer tarapin).

Lettered Tortoise of North America: *Emys sculpta.*

Green Turtle: *Chelone mydas.* (The edible variety much consumed in Seychelles.)

Loggerhead Turtle: *Thalassochelys caretta.* (I do not know this species by sight.)

Hawksbill Turtle: *Chelone imbricata.* (The tortoise-shell variety.)

I have, etc.,

(Signed) W. E. Davidson,
Governor.

The Right Honourable
The Secretary of State
for the Colonies.

A Bee-disease due to a Protozoal Parasite (Nosema apis).

Dr. H. B. FANTHAM, F.Z.S., and Miss ANNIE PORTER, D.Sc., exhibited some diseased bees and combs infected with a minute pathogenic protozoal parasite, apparently the same as *Nosema apis* found by Zander in diseased bees in Bavaria. Microscopic preparations and drawings of the parasite, *Nosema apis*, were also shown, as well as healthy bees and combs in contrast. The material exhibited was obtained from Cambridgeshire and Hertfordshire in March, 1911. Some of the infected combs were brown in colour instead of the normal yellow (combs of the same age being compared), while the infected bees suffered from a sort of dry dysentery which rapidly proved fatal.

The pathogenic agent of this dry dysentery, *Nosema apis*, formed thousands of minute spores which fouled the hive, while infection was probably spread to new hives by hungry, weakly bees attempting to enter healthy hives. The spores, about 2 to 3μ by 4 to 6μ, were the resistant and cross-infective stages of the Protozoön. The parasite *Nosema apis* was closely allied to that of pébrine, the silkworm disease due to *Nosema bombycis*.

The trophozoite and pansporoblast stages of the *Nosema apis* had been observed in the gut-epithelium of the bee. Some spores with polar filaments extruded had also been found. It was very probable that the young, growing and multiplicative stages of the parasite were capable of killing the bees before the formation of spores had been attained, for dead bees were often found in which only young stages of the parasite could be detected, occurring especially in the chyle-stomach and intestine. Like *N. bombycis*, the bee-parasite was possibly capable of hereditary infection, as infected bee-larvæ and a dead infected queen had been found and examined. Maassen had recently found infected drones in Germany, but the infection in drones was stated to be limited to the intestine.

That *Nosema apis* was fatal to bees and allied Hymenoptera had been shown by the exhibitors by feeding healthy hive-bees, mason-bees, and wasps with honey infected with *Nosema* spores; also by placing hive-bees dead of the disease among healthy hive- and mason-bees and wasps, and by direct contamination of healthy bees with infected fæcal matter. In each case the insects experimented upon succumbed to the effects of *Nosema apis*. In Nature the method of infection is probably contaminative, healthy bees becoming infected by swallowing the spores of the parasite.

It should be noted that the virulence of the parasite appeared to vary in bees at different times of the year and in different localities. Bad seasons are usually followed by increase of disease. Some bees became chronics, forming reservoirs of spores and so acting as parasite-carriers.

The only certain destructive agent of the Microsporidian spores was fire, and all infected bees and hives, and any débris therefrom should be most carefully burned.

In the opinion of the exhibitors, the Microsporidian parasite, *Nosema apis*, had been responsible for much of the bee-disease recorded in this country since 1906, especially in 1906, 1907, and 1911. The exhibitors first noticed the parasite in 1906 in diseased bees obtained from the Isle of Wight; its full significance was grasped in 1907, but owing to the difficulty of obtaining material the exhibitors' results were not published. As much attention was now being directed to "bee-disease," the exhibitors briefly recorded their observations. It was not asserted that microsporidiosis was the only disease of bees current in Great Britain at present, as Dr. Malden had investigated a bacillary infection in bees, the parasite being called *Bacillus pestiformis apis*. "Foul brood" also was a well-known and separate disease.

Microsporidiosis (due to *Nosema apis*) had probably been introduced from the Continent into British apiaries.

Other parasites found in bees—chiefly in the gut—by the exhibitors were various species of Gregarines, a Flagellate apparently belonging to the genus *Crithidia*, a new Amœba (*Entamœba apis*) very like *Entamœba coli* of the human intestine, a Spirochæte, and various Fungi.

PAPERS.

29. Contributions to the Anatomy and Systematic Arrangement of the Cestoidea. By Frank E. Beddard, M.A., F.R.S., F.Z.S., Prosector to the Society.

[Received and Read April 4th, 1911.]

(Text-figures 148–159.)

I. On some Mammalian Cestoidea.

I propose to communicate to the Society from time to time reports upon the species of Cestoidea which have been collected, and are being at present collected, from animals which have died in the Society's Gardens. The collection in my hands is the result of nearly two years' examination of (necessarily) a great number of animals, but does not contain as yet a very large number of species, either of known forms or of those which I believe to be undescribed. Tapeworms are by no means so common as other parasitic worms, particularly Nematodes, which are most abundant among the animals in the Gardens. Of the forms which I have identified as belonging to well-known species, I propose at some date to give a complete list, which will be useful, not only as indicating the species which are most abundant in the captive animals, but as extending the range of hosts. At present I could hardly give a long enough list to